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ABSTRACT: The objective was to estimate breed, heterosis, and recombination effects on pig reproductive traits in two different four-breed composite populations. Breeds included Yorkshire, Landrace, Large White, and Chester White in Exp. 1 and Duroc, Hampshire, Pietrain, and Spot in Exp. 2. Data were recorded on purebred pigs, two-breed cross pigs, and pigs from generations F_1 through F_6, where F_1 pigs were the first generation of a four-breed cross. Litter traits were considered a trait of the gilt. There were 868 first parity litters in Exp. 1 and 865 in Exp. 2. Direct heterosis significantly increased sow weight at 110 d of gestation and litter weight at 14 and 28 d (weaning) in both experiments. Direct heterosis significantly increased number of nipples, weight at puberty, lactation weight loss, litter size, and litter birth weight in Exp. 2. Gestation length in Exp. 1 and age at puberty in Exp. 1 and Exp. 2 were significantly decreased by direct heterosis. Maternal heterosis significantly increased age at puberty in Exp. 2 and decreased sow weight at 110 d of gestation in Exp. 1. Recombination significantly increased sow weight at 110 d of gestation and tended to increase total number born and litter birth weight in Exp. 1. Recombination significantly decreased age at puberty in Exp. 2. Litter heterosis significantly increased number of pigs at 14 and 28 d; litter weights at birth, 14, and 28 d; and tended to increase lactation weight loss in Exp. 1. Litter heterosis decreased litter size in Exp. 2. Maternal heterosis and recombination effects had a sampling correlation of –0.97 in Exp. 1 and –0.91 in Exp. 2 for number of fully formed pigs. Therefore, maternal heterosis and recombination effects were summed, and their net effect was tested. This net effect tended to increase number of nipples, lactation weight loss, and litter birth weight and significantly increased number of fully formed pigs in Exp. 1. Direct, maternal, and litter heterosis and recombination effects significantly influenced reproductive traits.

Key Words: Cytoplasm, Epistasis, Pigs, Recombination, Reproduction, Variance Components

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Introduction

The optimal use of genetic resources and the comparative efficiency of various crossbreeding systems is determined by differences among breed effects relative to magnitudes of heterosis and recombination effects. Estimation of these genetic effects, therefore, provides essential information to guide efficient use of genetic resources in crossbreeding systems. Many estimates of breed and heterosis effects on reproductive traits of pigs have been reported, but estimates of recombination or epistatic effects are scarce. Recombination loss, hereafter referred to as recombination, is the breakup of epistatic effects during meiosis to form nonparental interlocus combinations of alleles in gametes of crossbred parents (Dickerson, 1973). Recombination as defined by Dickerson (1973) included additive × additive effects only. With regards to reproductive traits of pigs, Bidanel (1993) reported a significant dominance × dominance effect on sow weight loss during lactation, and Bass et al. (1992) reported a significant recombination effect on litter birth weight.

The experimental objective was to simultaneously estimate breed, heterosis, and recombination effects on reproductive traits of pigs.

Materials and Methods

General Experimental Design

Population. Eight populations of purebred pigs were established for this research at the U.S. Meat Animal Research Center, Clay Center, NE (Young et al., 1986). Pigs in Exp. 1 farrowed about 125 litters during February of each year and included offspring derived from Yorkshire, Landrace, Large White, and Chester White breeds. About 125 litters were born during October of

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each year in Exp. 2 and included progeny derived from Duroc, Hampshire, Pietrain, and Spot breeds. In 1980, two-breed crosses were produced by mating Chester White boars to Large White gilts and Yorkshire boars to Landrace gilts in Exp. 1 and reciprocal crosses of Duroc × Pietrain and Hampshire × Spot in Exp. 2. In 1981, the first generation of four-breed crosses (F_1) was produced. Each crossbred population was inter se mated thereafter, producing F_2, F_3, F_4, F_5, and F_6 litters in 1982, 1983, 1984, 1985, and 1986, respectively. Purebred pigs were produced contemporary to crossbred pigs from 1980 through 1984. In 1985, all possible two-breed crosses were produced contemporary to F_5 pigs within each experiment. In 1986, F_6 pigs were born contemporary to four-breed cross F_1 pigs created from all possible matings of two-breed crosses. Appendices illustrate breed-types on which data were recorded. Only first-parity females farrowed during the experiment. Reproductive data were not recorded on gilts born in 1986.

Management and Data Collection. Management was described by Cassady et al. (2002). Pigs were reared by their own dams, except in a few cases when cross-fostering was allowed. Less than 1% of pigs and less than 3% of litters were affected by cross fostering. Neither birth dam nor foster dam were given credit for a foster pig at 14 d and weaning. Number of nipples was recorded on boars and gilts at birth. Access to creep feed was provided after 14 d. At 28 d, pigs were weaned and moved to a nursery room. Pigs were assigned to nursery pens by litter. However, small litters were sometimes combined into a common nursery pen. At 63 d of age, pigs were moved to a growing/finishing building. Gilts were penned in groups of 20 by breed type. Gilts were weighed every 28 d from 70 d until 9 mo of age. Beginning at approximately 154 d of age, gilts were allowed daily physical exposure to a mature boar. Age at puberty was recorded as the age when a gilt first exhibited an immobilized stance in response to a boar. Weight at puberty was approximated by calculating ADG during the time period for which estrus was recorded and extrapolating from the weigh date which was recorded closest to date of puberty.

All gilts were naturally mated, and gestation length was recorded as days from mating to farrowing. At 110 d of gestation, females were weighed and moved to a farrowing crate. At farrowing, numbers of pigs fully formed, born live, stillborn, and mummified were recorded. Litter birth weight was a summation of fully formed pig birth weights. Litter weights at 14 d and weaning (28 d) were summations of pig weights at those ages. Sow weights were recorded at weaning. The difference between sow weight at 110 d of gestation and weaning was recorded as lactation weight loss. Thus, lactation weight loss included gravid uterine weight as well as loss of body weight. Gilts were fed 1.6 kg per day from 0 to 80 d of gestation and 2.5 kg per day from 81 day to farrowing of a corn-soybean meal based diet that had a calculated ME of 3.44 Mcal/kg and a CP of 14.0%. During lactation, sows were provided ad libitum access to a corn-soybean meal based diet that had a calculated ME of 3.39 Mcal/kg and a CP of 17.2%.

Statistical Analysis. Genetic expectations for each breed type were developed considering direct, maternal, paternal, and maternal grandam breed effects; direct, maternal, and paternal heterosis effects; and direct, maternal, and paternal recombination effects (Cassady et al., 2002). All traits were analyzed as traits of the gilt (except number of nipples was also recorded on boars), that is, direct effects (breed, heterosis, and recombination) refer to the gilt. As purebred gilts produced either purebred or crossbred litters in 1980, an additional fixed genetic effect of litter heterosis (h^L) was fitted for traits recorded on pregnant females. Thus, h^L, h^I, and h^M are litter, direct (dam of the litter), and maternal (grandam of the litter) heterosis effects, respectively. Covariate values for litter heterosis were 0 for purebred litters, 1 for two-breed and F_1 litters, and 0.75 for F_2, F_3, F_4, F_5, and F_6 litters. Estimable functions were derived and constraints imposed as described by Cassady et al. (2002). The estimable function for litter heterosis was unbiased. Estimates of direct, maternal, and maternal grandam breed effects are deviations from Yorkshire in Exp. 1 and Duroc in Exp. 2.

Genetic parameters were estimated using the MTDFREML program described by Boldman et al. (1995). Farrowing group was included as a fixed effect in all models, while sex was included as a fixed effect only for analysis of number of nipples. Fixed genetic effects of estimable functions were fitted as linear covariates (Robison et al., 1981). Regression analysis was preferable to use of linear contrasts between means of breed types because multiple regression coefficients provided a simultaneous weighting of all existing data (MacNeil et al., 1982). Random effects initially included animal genetic, maternal genetic, common environment (litter of birth), and residual. All known pedigree relationships back to grandparents of 1980-born litters were included. Maternal genetic and common environmental effects were tested separately by comparing –2 residual log likelihoods of full and reduced (excluding the random effect of interest) models. Neither maternal genetic nor common environmental effects were significant for any trait, and these two random effects were deleted from all models.

In separate analyses, cytoplasmic effects were estimated for each trait from data collected in generations F_3, F_4, F_5, and F_6 (composite pigs). Given the full model previously described, composite pigs have identical genetic expectations with exception of their source of cytoplasm (Table 2, Cassady et al., 2002). In Exp. 1, composite pigs had either Landrace or Large White cytoplasm. In Exp. 2, composite pigs had either Duroc, Hampshire, Pietrain, or Spot cytoplasm. In Exp. 1, weight at 110 d of gestation differed significantly due to source of cytoplasm. In Exp. 2, pigs with Duroc cytoplasm had significantly heavier litter weights at 14 d ($P < 0.05$) and tended to have more pigs and greater litter weaning weights ($P < 0.1$) than pigs with Pietrain or Hampshire

Table 1. Number of observations, means, variance components, and genetic parameters for Experiments 1 and 2[a]

Trait	Experiment 1 n	$\bar{x}$	σ_p^2	σ_a^2	h^2	Experiment 2 n	$\bar{x}$	σ_p^2	σ_a^2	h^2
Number of nipples	8,351	14.06	1.03	0.38	0.37 ± 0.03	7,969	13.32	1.17	0.50	0.43 ± 0.03
Puberty										
Age, d	2,132	206.21	873.21	271.43	0.31 ± 0.05	2,061	203.13	670.99	215.36	0.32 ± 0.05
Weight, kg	2,132	102.87	181.90	73.11	0.40 ± 0.05	2,059	99.53	132.54	51.39	0.39 ± 0.05
Gestation length, d	866	114.50	2.16	1.08	0.50 ± 0.07	861	113.71	2.08	1.13	0.54 ± 0.07
Sow weights, kg										
110 d of gestation	868	157.06	214.58	68.54	0.32 ± 0.07	861	153.96	175.10	57.31	0.33 ± 0.07
Weaning	825	139.07	227.99	95.30	0.42 ± 0.08	809	137.13	216.96	57.58	0.27 ± 0.07
Lactation weight loss	824	–18.16	144.29	22.58	0.16 ± 0.06	807	–16.88	129.54	18.52	0.14 ± 0.06
Litter size										
NFF	868	8.86	6.28	2.15	0.34 ± 0.07	865	8.35	5.38	1.24	0.23 ± 0.07
NBA	868	8.32	6.50	1.92	0.30 ± 0.07	865	7.77	5.63	1.01	0.18 ± 0.07
ND14	868	7.27	7.40	1.50	0.20 ± 0.07	865	6.34	6.59	0.62	0.09 ± 0.06
NW	868	7.17	7.30	1.50	0.21 ± 0.07	865	6.02	6.45	0.65	0.10 ± 0.06
Litter weights, kg										
Birth	868	11.17	9.59	3.14	0.33 ± 0.07	865	11.03	7.94	1.96	0.25 ± 0.07
14 d	868	25.36	82.74	18.75	0.23 ± 0.07	865	21.26	70.15	7.86	0.11 ± 0.06
Weaning (d 28)	868	45.28	228.73	57.75	0.25 ± 0.07	865	37.73	202.19	27.68	0.14 ± 0.06

[a]n = number of observations, $\bar{x}$ = phenotypic mean, σ_p^2 = phenotypic variance corrected for fixed effects, σ_a^2 = genetic variance due to direct effects, h^2 = proportion of the phenotypic variance due to σ_a^2, and NFF, NBA, ND14, and NW = number of pigs fully formed, born live, live at 14 d, and weaned, respectively.

cytoplasm. The number of traits for which a significant cytoplasmic effect was detected did not exceed that which may be expected due to chance. Thus, cytoplasmic effects were excluded from all models.

Results

It was necessary to delete genetic effects from the design matrix of the full genetic model to obtain solutions. The same constraints were imposed as described by Cassady et al. (2002); therefore, expectations of estimable functions were identical to the companion manuscript. These constraints and resulting expectations should be considered as one interprets results. An additional effect of litter heterosis was fitted for traits recorded on pregnant females. The estimable function for litter heterosis did not include other genetic effects.

Number of observations, means, variance components, and genetic parameters for Exp. 1 and Exp. 2 are in Table 1. Heritabilities were similar between experiments for number of nipples, age at puberty, weight at puberty, gestation length, weight at 110 d of gestation, and lactation weight loss. In Exp. 1, heritability estimates of litter traits were greater than typically reported. No explanation other than sampling is apparent. However, Exp. 2 heritability estimates were similar to literature estimates.

Sampling correlations among estimable functions for number of fully formed pigs are given in Tables 2 and 3 for Exp. 1 and Exp. 2, respectively. Correlations among effects depend on structure of the data and, thus, were similar for all traits within experiment. Correlations which included maternal or maternal grandam breed effects were inconsistent between Exp. 1 and Exp. 2. This discrepancy was due to differences in the way pigs born in 1979 were mated in each experiment. Due to a limited number of Yorkshire and Chester White females, only Landrace and Large White females produced two-breed cross pigs during 1980 in Exp. 1. As a result, all F_1 pigs had either a Landrace or a Large White maternal grandam. In Exp 2, reciprocal crosses were made; thus, maternal and maternal grandam effects were contributed from all four breeds. These 1980-born litters provided the foundation for generations F_1 through F_6.

A large negative sampling correlation existed between maternal heterosis and recombination (–0.97, Table 2; –0.91, Table 3). As a consequence, estimates of maternal heterosis and recombination are greatly confounded. These two effects were summed to estimate their net effect which is provided in the last rows of Tables 4 through 7.

Number of nipples was influenced by direct, maternal, and maternal grandam breed effects in Exp. 1 and Exp. 2 (Tables 4 and 5). Direct heterosis significantly increased number of nipples in Exp. 2; however, when expressed as a percentage, the effect was small. Maternal heterosis and recombination did not significantly affect number of nipples in either experiment. However, net effect of maternal heterosis and recombination tended to increase number of nipples in Exp. 1.

Direct breed effects significantly affected age and weight at puberty in both experiments. Maternal breed effects influenced age and weight at puberty in Exp. 2 and weight at puberty in Exp. 1. Maternal grandam breed effects tended to differ for age at puberty in Exp.

Table 2. Sampling correlations among estimable functions for number of fully formed pigs in Experiment 1[a]

Estimable function	$g_L^{I'}$	$g_W^{I'}$	$g_C^{I'}$	$g_L^{M'}$	$g_W^{M'}$	$g_C^{M'}$	$g_L^{MG'}$	$g_W^{MG'}$	$g_C^{MG'}$	$h^{I'}$	$h^{M'}$	$r^{I'}$	$h^{L'}$
$g_L^{I'}$	1.00	0.50	0.41	−0.22	−0.15	−0.23	−0.04	−0.02	−0.04	0.27	−0.05	0.01	0.00
$g_W^{I'}$		1.00	0.57	0.09	−0.33	0.03	−0.23	−0.02	−0.40	0.23	−0.04	0.00	−0.01
$g_C^{I'}$			1.00	0.12	−0.22	−0.18	−0.23	0.01	−0.43	0.02	−0.01	0.00	0.01
$g_L^{M'}$				1.00	0.68	0.35	−0.94	−0.78	−0.40	0.04	0.74	−0.69	−0.21
$g_W^{M'}$					1.00	0.17	−0.65	−0.91	0.04	0.04	0.78	−0.73	−0.22
$g_C^{M'}$						1.00	−0.26	−0.18	−0.69	−0.01	0.04	−0.03	−0.01
$g_L^{MG'}$							1.00	0.82	0.44	−0.14	−0.74	0.71	0.19
$g_W^{MG'}$								1.00	0.16	−0.15	−0.82	0.79	0.21
$g_C^{MG'}$									1.00	−0.01	−0.03	0.02	0.00
$h^{I'}$										1.00	−0.01	−0.08	−0.50
$h^{M'}$											1.00	−0.97	−0.26
$r^{I'}$												1.00	0.28
$h^{L'}$													1.00

[a]$g_i^{I'}$, $g_i^{M'}$, and $g_i^{MG'}$ are estimable functions for direct, maternal, and maternal grandam breed effects. Subscript i represents a breed associated with the effect. L = Landrace, W = Large White, and C = Chester White. $h^{I'}$, $h^{M'}$, and $h^{L'}$ are estimable functions for direct, maternal, and litter heterosis effects. $r^{I'}$ is an estimable function for the direct recombination effect.

2. Direct heterosis significantly decreased age at puberty in both experiments and increased weight at puberty in Exp. 2. Maternal heterosis increased age and weight at puberty, and recombination decreased age at puberty in Exp. 2. However, effects of maternal heterosis and recombination considered jointly were not significant in either experiment.

Direct breed effects for gestation length differed significantly in Exp. 2. Direct heterosis significantly decreased gestation length in Exp. 1. Direct breed effects for sow weight at 110 d of gestation significantly differed in both experiments. Maternal grandam breed effects differed, and maternal breed effects tended to differ in Exp. 1. Sow weight at 110 d of gestation increased due to direct heterosis in Exp. 1 and Exp. 2 and decreased due to maternal heterosis in Exp. 1. The negative effect of maternal heterosis was offset by a significant recombination effect, and their joint effect was not significant. Sow weight at weaning differed due to maternal and maternal grandam breed effects in Exp. 1 and direct breed effects in Exp. 2. Nonadditive genetic effects did not significantly influence sow weight at weaning in either experiment. Breed effects did not differ significantly for lactation weight loss in Exp. 1 or Exp. 2. Direct heterosis significantly increased lactation weight loss in Exp. 2. Litter heterosis and the net effect of maternal heterosis and direct recombination tended to increase lactation weight loss in Exp. 1.

Estimates and standard errors of estimable functions for litter traits in Exp. 1 and Exp. 2 are provided in

Table 3. Sampling correlations among estimable functions for number of fully formed pigs in Experiment 2[a]

Estimable function	$g_H^{I'}$	$g_P^{I'}$	$g_S^{I'}$	$g_H^{M'}$	$g_P^{M'}$	$g_S^{M'}$	$g_H^{MG'}$	$g_P^{MG'}$	g_S^{MG}	$h^{I'}$	$h^{M'}$	$r^{I'}$	$h^{L'}$
$g_H^{I'}$	1.00	0.50	0.47	−0.43	−0.15	−0.17	−0.08	−0.11	−0.08	−0.02	−0.09	0.07	0.04
$g_P^{I'}$		1.00	0.50	−0.22	−0.44	−0.23	−0.02	−0.06	−0.02	−0.03	0.01	−0.02	0.02
$g_S^{I'}$			1.00	−0.19	−0.16	−0.42	−0.05	−0.09	−0.12	−0.01	−0.08	0.07	0.01
$g_H^{M'}$				1.00	0.41	0.22	−0.80	−0.29	−0.08	0.04	0.10	−0.11	−0.05
$g_P^{M'}$					1.00	0.41	−0.35	−0.79	−0.33	0.02	0.14	−0.14	−0.01
$g_S^{M'}$						1.00	−0.11	−0.28	−0.78	0.04	0.06	−0.08	−0.05
$g_H^{MG'}$							1.00	0.43	0.17	−0.03	−0.05	0.07	0.05
$g_P^{MG'}$								1.00	0.41	0.00	−0.18	0.18	0.01
$g_S^{MG'}$									1.00	−0.03	0.00	0.04	0.05
$h^{I'}$										1.00	−0.26	0.08	−0.55
$h^{M'}$											1.00	−0.91	−0.14
$r^{I'}$												1.00	0.17
$h^{L'}$													1.00

[a]$g_i^{I'}$, $g_i^{M'}$, and $g_i^{MG'}$ are estimable functions for direct, maternal, and maternal grandam breed effects. Subscript i represents a breed associated with the effect. H = Hampshire, P = Pietrain, and S = Spot. $h^{I'}$, $h^{M'}$, and $h^{L'}$ are estimable functions for direct, maternal, and litter heterosis effects. $r^{I'}$ is an estimable function for the direct recombination effect.

Table 4. Estimates and standard errors of estimable functions for reproductive traits in Experiment 1[a]

Estimable function[a]	Number of nipples	Age at puberty, d	Wt at puberty, kg	Gestation length, d	Sow wt 110 d gestation, kg	Sow wt at weaning, kg	Lactation wt loss, kg
F-value	2.88*	7.23***	8.34***	1.40	3.54*	1.38	1.45
$g_L^{I'}$	0.60 ± 0.24	–34.17 ± 8.90	–16.99 ± 4.27	–1.06 ± 0.64	13.13 ± 6.21	5.45 ± 6.60	7.09 ± 4.85
$g_W^{I'}$	0.53 ± 0.24	–5.05 ± 8.96	–0.43 ± 4.30	–1.34 ± 0.73	7.22 ± 7.06	–2.81 ± 7.60	6.71 ± 5.68
$g_C^{I'}$	0.10 ± 0.26	4.92 ± 9.12	2.40 ± 4.41	–0.62 ± 0.70	19.13 ± 6.71	9.22 ± 7.22	10.21 ± 5.26
F-value	2.64*	1.47	3.78**	0.43	2.58†	3.20*	0.60
$g_L^{M'}$	–0.03 ± 0.17	–5.11 ± 8.77	1.84 ± 3.92	–1.22 ± 1.43	–41.93 ± 15.15	–42.35 ± 15.47	6.54 ± 12.87
$g_W^{M'}$	0.15 ± 0.17	–9.47 ± 8.72	7.31 ± 3.90	–0.12 ± 1.39	–26.24 ± 14.74	–11.54 ± 15.10	–6.48 ± 12.55
$g_C^{M'}$	–0.30 ± 0.14	–14.76 ± 7.27	–5.81 ± 3.25	–0.46 ± 0.63	–5.30 ± 6.72	–7.41 ± 6.82	0.80 ± 5.89
F-value	2.19†	0.21	1.48	0.87	3.94*	2.64*	0.84
$g_L^{MG'}$	0.24 ± 0.15	–3.88 ± 7.25	–2.66 ± 3.30	1.49 ± 1.37	32.06 ± 14.44	36.83 ± 14.80	–9.24 ± 12.25
$g_W^{MG'}$	–0.07 ± 0.15	–0.39 ± 7.42	–6.61 ± 3.38	0.59 ± 1.28	23.86 ± 13.50	21.24 ± 13.78	–14.51 ± 11.43
$g_C^{MG'}$	0.21 ± 0.13	–4.13 ± 6.63	–3.85 ± 3.01	1.09 ± 0.71	–8.81 ± 7.47	3.86 ± 7.64	–9.85 ± 6.45
$h^{I'}$	0.04 ± 0.07	–12.87 ± 3.25***	–0.04 ± 1.49	–0.56 ± 0.26*	6.11 ± 2.70*	3.01 ± 2.78	3.54 ± 2.35
$h^{I'}$ %	0.3	–6.1	0.0	–0.5	3.9	2.2	–17.7
$h^{M'}$	–0.07 ± 0.21	–3.42 ± 8.73	5.31 ± 4.14	0.82 ± 1.30	–27.16 ± 13.18*	–16.45 ± 13.59	–7.70 ± 10.99
$r^{I'}$	0.42 ± 0.38	6.85 ± 14.09	–2.78 ± 6.90	–1.42 ± 1.57	33.13 ± 15.39*	15.63 ± 16.14	12.79 ± 12.35
$h^{L'}$				–0.10 ± 0.21	3.10 ± 2.17	–0.54 ± 2.24	3.39 ± 1.85†
$h^{M'} + r^{I'}$	0.35 ± 0.19†	3.43 ± 7.06	2.53 ± 3.47	–0.60 ± 0.48	5.97 ± 4.19	–0.82 ± 4.69	5.09 ± 2.93†

[a]$g_i^{I'}$, $g_i^{M'}$, and $g_i^{MG'}$ are estimable functions for direct, maternal, and maternal grandam breed effects. Subscript i represents a breed associated with the effect. L = Landrace, W = Large White, and C = Chester White. Estimates of direct, maternal, and maternal grandam breed effects are deviations from the effect of Yorkshire. F-values are a 3 degree of freedom F-test for direct, maternal, or maternal grandam breed effects. $h^{I'}$, $h^{M'}$, and $h^{L'}$ are estimable functions for direct, maternal, and litter heterosis effects. $r^{I'}$ is an estimable function for the direct recombination effect.

†$P < 0.10$, *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

Table 5. Estimates and standard errors of estimable functions for reproductive traits in Experiment 2[a]

Estimable function	Number of nipples	Age at puberty, d	Wt at puberty, kg	Gestation length, d	Sow wt 110 d gestation, kg	Sow wt at weaning, kg	Lactation wt loss, kg
F-value	8.45***	10.50***	25.33***	3.10*	6.50***	8.14***	0.64
$g_H^{I'}$	−0.07 ± 0.26	−28.04 ± 7.92	−11.25 ± 3.65	0.28 ± 0.62	−0.69 ± 5.42	−1.80 ± 5.98	1.89 ± 4.39
$g_P^{I'}$	−0.63 ± 0.25	−36.93 ± 7.46	−29.47 ± 3.42	1.43 ± 0.59	−18.16 ± 5.20	−21.82 ± 5.75	2.76 ± 4.24
$g_S^{I'}$	0.62 ± 0.25	−37.02 ± 7.75	−15.81 ± 3.56	1.45 ± 0.62	2.06 ± 5.46	4.60 ± 6.05	−2.98 ± 4.46
F-value	7.69***	3.00*	6.73***	0.26	0.23	0.41	0.09
$g_H^{M'}$	−0.71 ± 0.16	15.40 ± 6.93	7.73 ± 3.03	−0.08 ± 0.70	3.97 ± 6.90	3.80 ± 7.93	0.23 ± 6.28
$g_P^{M'}$	−0.17 ± 0.16	17.98 ± 6.77	9.13 ± 2.97	−0.16 ± 0.68	3.63 ± 6.65	8.17 ± 7.59	−2.38 ± 5.97
$g_S^{M'}$	−0.40 ± 0.16	15.83 ± 7.16	13.45 ± 3.12	−0.61 ± 0.70	4.82 ± 6.88	5.58 ± 7.88	0.45 ± 6.23
F-value	4.60**	2.32†	1.53	0.25	0.63	0.75	0.08
$g_H^{MG'}$	0.49 ± 0.13	−6.51 ± 5.65	−4.66 ± 2.50	0.06 ± 0.61	−6.76 ± 5.94	−7.80 ± 6.79	0.03 ± 5.32
$g_P^{MG'}$	0.28 ± 0.13	−13.62 ± 5.32	−3.19 ± 2.36	0.03 ± 0.59	−4.81 ± 5.67	−5.06 ± 6.42	−1.40 ± 4.98
$g_S^{MG'}$	0.22 ± 0.14	−9.29 ± 5.58	−4.16 ± 2.46	0.50 ± 0.63	−5.79 ± 6.07	−8.13 ± 6.90	1.23 ± 5.39
$h^{I'}$	0.19 ± 0.07**	−21.22 ± 2.72***	2.68 ± 1.21*	−0.09 ± 0.23	9.67 ± 1.96***	−0.50 ± 2.26	8.48 ± 2.14***
$h^{I'}$ %	1.5	−10.0	2.7	−0.1	6.3	−0.4	−55.1
$h^{M'}$	−0.03 ± 0.21	18.26 ± 7.09**	5.31 ± 3.23†	−0.46 ± 0.64	−6.17 ± 6.05	−4.89 ± 7.02	−0.78 ± 5.49
$r^{I'}$	0.28 ± 0.38	−24.66 ± 11.54*	−7.91 ± 5.38	0.39 ± 0.89	10.42 ± 7.82	9.06 ± 8.84	−1.30 ± 6.54
$h^{L'}$				−0.26 ± 0.19	1.63 ± 1.86	−0.93 ± 2.19	2.66 ± 1.73
$h^{M'} + r^{I'}$	0.25 ± 0.20	−6.40 ± 5.98	−2.60 ± 2.80	−0.07 ± 0.44	4.25 ± 3.55	4.17 ± 3.79	−0.52 ± 2.52

[a] $g_i^{I'}$, $g_i^{M'}$, and $g_i^{MG'}$ are estimable functions for direct, maternal, and maternal grandam breed effects. Subscript i represents a breed associated with the effect. H = Hampshire, P = Pietrain, and S = Spot. Estimates of direct, maternal, and maternal grandam breed effects are deviations from the effect of Duroc. F-values are a 3 degree of freedom F-test for direct, maternal, or maternal grandam breed effects. $h^{I'}$, $h^{M'}$, and $h^{L'}$ are estimable functions for direct, maternal, and litter heterosis effects. $r^{I'}$ is an estimable function for the direct recombination effect.

†$P < 0.10$, *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

Table 6. Estimates and standard errors of estimable functions for litter size and weight traits in Experiment 1[a]

Estimable function	NFF	NBA	ND14	NW	Birth wt	d 14 wt	Weaning wt
F-value	2.89*	2.22†	0.79	0.71	5.24**	1.32	1.15
$g_L^{I'}$	1.96 ± 1.07	2.17 ± 1.07	1.69 ± 1.11	1.56 ± 1.10	4.84 ± 1.31	5.46 ± 3.74	6.91 ± 6.27
$g_W^{I'}$	1.62 ± 1.21	1.72 ± 1.22	0.78 ± 1.27	0.73 ± 1.26	2.64 ± 1.49	2.62 ± 4.28	4.55 ± 7.17
$g_C^{I'}$	3.21 ± 1.16	2.61 ± 1.16	0.48 ± 1.20	0.26 ± 1.19	3.76 ± 1.42	−2.21 ± 4.04	−4.82 ± 6.78
F-value	0.75	0.79	0.40	0.48	0.68	0.61	0.55
$g_L^{M'}$	−3.41 ± 2.58	−2.91 ± 2.65	−1.57 ± 2.87	−1.82 ± 2.85	−3.45 ± 3.20	2.45 ± 9.57	4.57 ± 15.84
$g_W^{M'}$	−3.53 ± 2.51	−3.47 ± 2.58	−2.26 ± 2.79	−2.36 ± 2.77	−4.37 ± 3.11	−3.32 ± 9.30	−2.25 ± 15.41
$g_C^{M'}$	−2.75 ± 1.14	0.43 ± 1.18	0.71 ± 1.30	0.79 ± 1.28	−0.16 ± 1.42	5.12 ± 4.30	8.68 ± 7.10
F-value	3.07*	2.74	1.16	1.28	1.76	0.68	0.94
$g_L^{MG'}$	2.60 ± 2.46	2.07 ± 2.53	0.93 ± 2.73	1.22 ± 2.71	2.40 ± 3.05	−2.33 ± 9.10	−4.51 ± 15.08
$g_W^{MG'}$	1.78 ± 2.30	1.68 ± 2.36	0.97 ± 2.55	1.11 ± 2.54	1.87 ± 2.85	−0.16 ± 8.51	−4.53 ± 14.10
$g_C^{MG'}$	−2.34 ± 1.27	−2.55 ± 1.31	−2.04 ± 1.43	−2.02 ± 1.41	−2.30 ± 1.58	−6.48 ± 4.74	−11.44 ± 7.84
$h^{I'}$	−0.05 ± 0.46	0.32 ± 0.47	0.67 ± 0.51	0.64 ± 0.51	0.54 ± 0.57	3.60 ± 1.71*	6.80 ± 2.83*
$h^{I'}$ %	−0.6	3.8	9.1	8.7	4.9	13.7	14.8
$h^{M'}$	−2.99 ± 2.25	−2.67 ± 2.30	−3.07 ± 2.46	−3.18 ± 2.45	−3.86 ± 2.79	−6.43 ± 8.23	−7.78 ± 13.67
$r^{I'}$	4.60 ± 2.64†	3.80 ± 2.67	4.03 ± 2.80	4.20 ± 2.78	5.56 ± 3.26†	9.59 ± 9.41	13.39 ± 15.72
$h^{L'}$	0.43 ± 0.37	0.54 ± 0.38	0.80 ± 0.41*	0.92 ± 0.41*	1.30 ± 0.46**	4.13 ± 1.37**	6.98 ± 2.26**
$h^{M'} + r^{I'}$	1.61 ± 0.74*	1.13 ± 0.73	0.96 ± 0.70	1.02 ± 0.70	1.70 ± 0.91†	3.16 ± 2.41	5.61 ± 4.13

[a]NFF, NBA, ND14, and NW = number of pigs fully formed, born live, live at 14 d, and weaned, respectively. Birth wt, 14 d wt, and weaning wt are litter weights at birth, 14 d, and weaning (28 d), respectively. $g_i^{I'}$, $g_i^{M'}$, and $g_i^{MG'}$ are estimable functions for direct, maternal, and maternal grandam breed effects. Subscript i represents a breed associated with the effect. L = Landrace, W = Large White, and C = Chester White. Estimates of direct, maternal, and maternal grandam breed effects are deviations from the effect of Yorkshire. F-values are a 3 degree of freedom F-test for direct, maternal, or maternal grandam breed effects. $h^{I'}$, $h^{M'}$, and $h^{L'}$ are estimable functions for direct, maternal, and litter heterosis effects. $r^{I'}$ is an estimable function for the direct recombination effect.

†$P < 0.10$, *$P < 0.05$, **$P < 0.01$.

Tables 6 and 7, respectively. In Exp. 1, direct breed effects differed for number of fully formed pigs and litter birth weight and tended to differ for number of pigs born live. Maternal grandam effects differed for number of fully formed pigs born. Direct heterosis increased litter weights at 14 d and weaning. Recombination tended to increase number of fully formed pigs, and the net effects of maternal heterosis and recombination significantly increased number of fully formed pigs. Litter heterosis increased litter weights at all ages and increased number of pigs at 14 d and weaning. In Exp. 2, direct breed effects tended to differ for all litter traits. Direct heterosis significantly increased all litter traits. Litter heterosis effects were negative for litter traits except litter weight at weaning. Maternal heterosis, recombination, and their net effect did not significantly influence litter traits in Exp. 2.

Discussion

Heritability estimates were within the range of estimates and generally consistent with weighted averages reported in a review by Lamberson (1991), with the exception of litter traits in Exp. 1. Estimates of percentage direct heterosis in Exp. 1 were generally consistent with estimates from the North Central Regional Project (Johnson, 1980). Estimates of percentage direct heterosis in Exp 2 were greater than expected.

Baas et al. (1992) estimated heterosis and recombination effects for litter size, litter weight, and lactation weight loss in Hampshire and Landrace using F_1, F_2, F_3, and backcross animals. Effects were estimated by contrasting means among breed types. A significant decrease in litter weight due to recombination was reported. As in the present study, standard errors of recombination effects on litter size were large.

Bidanel (1993) estimated dominance and epistatic effects in Large White and Meishan using a two-breed diallel with backcrosses. Data were analyzed by multiple regression assuming a model similar to that described by Koch et al. (1985). An animal model was used to account for relationships among animals. A simple dominance model provided the lowest mean square error for all traits related to litter size. A significant additive × additive effect was reported for sow feed consumption per pig weaned. Bidanel (1993) discussed a number of limitations associated with estimation of epistatic effects, but did not mention sampling correlations among effects. Cunningham and Connolly (1989) and Cassady et al. (2002) discuss correlations among estimable functions. Ignoring these correlations may lead to improper conclusions regarding genetic effects.

Standard errors of estimable functions for reproductive traits were large. Greater precision would have occurred if one experiment was eliminated and the remaining experiment doubled in size. A proportion of this expanded population should have been devoted to making backcrosses. Backcrosses would have reduced correlations among estimable functions and decreased standard errors. In addition, use of reciprocal crosses

Table 7. Estimates and standard errors of estimable functions for litter size and weight traits in Experiment 2[a]

Estimable function	NFF	NBA	ND14	NW	Birth wt	d 14 wt	Weaning wt
F-value	2.57†	2.66*	7.39***	7.63***	2.56†	4.14**	5.11**
$g_H^{I'}$	−0.89 ± 0.92	−0.50 ± 0.92	−1.30 ± 0.95	−1.37 ± 0.95	−1.89 ± 1.12	−3.44 ± 3.15	−5.57 ± 5.42
$g_P^{I'}$	−2.26 ± 0.89	−2.23 ± 0.89	−2.72 ± 0.92	−2.71 ± 0.91	−2.97 ± 1.08	−6.75 ± 3.03	−13.24 ± 5.22
$g_S^{I'}$	−1.90 ± 0.93	−1.73 ± 0.93	−4.31 ± 0.97	−4.38 ± 0.96	−1.80 ± 1.13	−10.70 ± 3.18	−19.96 ± 5.47
F-value	0.73	1.20	1.67	2.13†	1.07	1.10	1.28
$g_H^{M'}$	1.42 ± 1.24	1.25 ± 1.28	1.49 ± 1.41	1.78 ± 1.39	1.67 ± 1.50	4.02 ± 4.58	8.34 ± 7.75
$g_P^{M'}$	1.14 ± 1.19	1.40 ± 1.22	1.81 ± 1.34	1.79 ± 1.32	0.65 ± 1.44	4.48 ± 4.35	6.30 ± 7.38
$g_S^{M'}$	1.40 ± 1.23	2.27 ± 1.27	2.97 ± 1.39	3.30 ± 1.38	2.27 ± 1.49	7.86 ± 4.54	14.00 ± 7.69
F-value	0.57	0.92	0.46	0.62	0.71	0.31	0.34
$g_H^{MG'}$	−1.38 ± 1.06	−1.47 ± 1.09	−1.16 ± 1.19	−1.30 ± 1.17	−1.28 ± 1.28	−3.08 ± 3.87	−5.20 ± 6.57
$g_P^{MG'}$	−0.44 ± 1.00	−0.80 ± 1.03	−0.55 ± 1.11	−0.52 ± 1.10	0.29 ± 1.22	−1.62 ± 3.62	0.11 ± 6.15
$g_S^{MG'}$	−0.23 ± 1.08	−1.30 ± 1.11	−0.93 ± 1.20	−1.07 ± 1.19	−0.79 ± 1.31	−2.62 ± 3.93	−2.70 ± 6.66
$h^{I'}$	2.68 ± 0.41***	2.60 ± 0.43***	2.85 ± 0.47***	2.81 ± 0.47***	3.73 ± 0.50***	9.36 ± 1.53***	15.13 ± 2.59***
$h^{I'}$ %	36.5	38.3	51.9	51.9	38.3	48.2	42.9
$h^{M'}$	1.04 ± 1.08	1.28 ± 1.11	0.95 ± 1.21	0.68 ± 1.19	0.64 ± 1.31	3.10 ± 3.93	3.15 ± 6.67
$r^{I'}$	−1.50 ± 1.34	−1.82 ± 1.35	−1.33 ± 1.41	−1.00 ± 1.40	−0.74 ± 1.64	−3.53 ± 4.63	−1.97 ± 7.95
$h^{L'}$	−0.78 ± 0.33*	−0.67 ± 0.34*	−0.79 ± 0.37*	−0.61 ± 0.37*	−0.18 ± 0.40	−0.17 ± 0.12	0.21 ± 2.05
$h^{M'} + r^{I'}$	−0.46 ± 0.57	−0.54 ± 0.55	−0.38 ± 0.52	−0.32 ± 0.52	−0.10 ± 0.71	0.43 ± 1.76	1.18 ± 3.12

[a]NFF, NBA, ND14, and NW = number of pigs fully formed, born live, live at 14 d, and weaned, respectively. Birth wt, 14 d wt, and weaning wt are litter weights at birth, 14 d, and weaning (d 28), respectively. $g_i^{I'}$, $g_i^{M'}$, and $g_i^{MG'}$ are estimable functions for direct, maternal, and maternal grandam breed effects. Subscript i represents a breed associated with the effect. H = Hampshire, P = Pietrain, and S = Spot. Estimates of direct, maternal, and maternal grandam breed effects are deviations from the effect of Duroc. F-values are a 3 degree of freedom F-test for the direct, maternal, or maternal grandam breed effects. $h^{I'}$, $h^{M'}$, and $h^{L'}$ are estimable functions for direct, maternal, and litter heterosis effects. $r^{I'}$ is an estimable function for the direct recombination effect.

†$P < 0.10$, *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

among purebred animals in Exp. 1, as in Exp. 2, would have provided balanced correlations of maternal and maternal grandam effects with each other and with other genetic effects. The aforementioned suggestions would have improved the experiment; however Bidanel (1993) estimated that 14,000 litters are required to show an additive × additive effect of 0.5 pigs with a type I error rate of 5% and a power of 90%. Few, if any, research facilities exist which are capable of doing an experiment of such magnitude.

Implications

Estimates of genetic effects on reproductive traits of pigs are useful to evaluate breeds and to develop efficient crossbreeding systems. Reproductive traits of gilts were influenced by breed of gilt, but seldom by breed of dam or maternal grandam. Landrace, Large White, Yorkshire, and Chester White gilts were more productive carrying crossbred rather than purebred litters, but the opposite situation tended to occur for Duroc, Hampshire, Pietrain, and Spot gilts. Crossbred gilts were younger at puberty, weighed more at farrowing, and produced larger, heavier litters to weaning than purebred gilts. Gilts raised by purebred or crossbred dams had similar levels of performance. Relative to gilts by purebred parents, new allelic combinations among genes exist in gilts by crossbred sires and dams. New combinations had few significant effects on reproductive traits, but effects tended to be favorable for white breeds that are widely used by the industry to produce F_1 gilts.

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Appendix

Appendix Table 1. Least-squares means and standard errors of breed types for number of nipples, age at puberty, and weight at puberty in Experiment 1

Breed type[a]	Number of nipples	Age at puberty, d	Weight at puberty, kg
Y × Y	13.50 ± 0.06	226.9 ± 2.4	106.2 ± 1.1
L × L	14.35 ± 0.06	188.4 ± 2.3	92.6 ± 1.1
W × W	14.16 ± 0.06	210.7 ± 2.3	106.1 ± 1.1
C × C	13.48 ± 0.07	218.7 ± 2.7	101.5 ± 1.3
Y × L	14.30 ± 0.10	192.0 ± 4.4	98.0 ± 2.0
L × Y	13.84 ± 0.22	202.9 ± 9.9	101.9 ± 4.5
Y × W	14.07 ± 0.19	198.1 ± 8.9	99.9 ± 4.1
W × Y	13.90 ± 0.22	213.0 ± 9.8	102.2 ± 4.5
L × W	14.29 ± 0.24	187.9 ± 11.0	102.7 ± 5.1
W × L	13.94 ± 0.22	182.0 ± 9.4	91.7 ± 4.4
W × C	13.71 ± 0.23	197.0 ± 9.7	107.0 ± 4.5
C × L	13.89 ± 0.21	185.2 ± 10.1	99.5 ± 4.7
L × C	13.67 ± 0.22	185.3 ± 9.1	95.2 ± 4.2
C × Y	13.90 ± 0.18	214.3 ± 9.0	106.6 ± 4.1
Y × C	13.60 ± 0.21	200.7 ± 11.3	97.6 ± 5.2
C × W	13.80 ± 0.10	205.3 ± 4.6	110.1 ± 2.1
YL × CW	13.76 ± 0.13	200.5 ± 5.1	103.6 ± 2.4
YL × WC	14.17 ± 0.21	184.2 ± 9.0	101.4 ± 4.2
YW × CL	14.18 ± 0.21	177.7 ± 8.7	102.8 ± 4.1
YW × LC	14.04 ± 0.21	187.1 ± 9.1	104.8 ± 4.2
LW × CY	14.11 ± 0.21	199.3 ± 10.2	101.9 ± 4.7
LW × YC	14.22 ± 0.22	187.0 ± 9.9	98.7 ± 4.6

CW × YL	14.03 ± 0.12	204.4 ± 4.7	108.0 ± 2.2
CW × LY	13.83 ± 0.19	218.8 ± 8.9	116.8 ± 4.1
CL × YW	13.81 ± 0.22	205.1 ± 9.2	106.9 ± 4.3
CL × WY	14.20 ± 0.25	197.7 ± 12.6	113.7 ± 5.7
CY × LW	13.97 ± 0.28	181.7 ± 10.9	105.0 ± 5.0
CY × WL	14.19 ± 0.21	204.9 ± 8.8	114.7 ± 4.1
F_2[b]	13.91 ± 0.16	204.5 ± 6.3	102.0 ± 3.0
F_2[c]	14.11 ± 0.16	209.4 ± 6.0	101.1 ± 2.8
F_3	14.39 ± 0.06	206.2 ± 2.2	104.7 ± 1.1

[a]Y = Yorkshire, L = Landrace, W = Large White, and C = Chester White. The first letter indicates breed of sire and the second letter indicates breed of dam. F_3, F_4, F_5, and F_6 were pooled. Progeny of reciprocal two-breed dams were classified separately to account for maternal grandam breed effects, but progeny of reciprocal two-breed cross sires were pooled.
[b]F_2 animals with YL maternal grandams.
[c]F_2 animals with CW maternal grandams.

Appendix Table 2. Least-squares means and standard errors of breed types for number of nipples, age at puberty, and weight at puberty in Experiment 2

Breed type[a]	Number of nipples	Age at puberty, d	Weight at puberty, kg
H × H	13.04 ± 0.06	209.5 ± 2.3	98.8 ± 1.1
D × D	13.04 ± 0.06	234.3 ± 2.2	109.2 ± 1.0
P × P	12.57 ± 0.06	204.8 ± 2.2	86.3 ± 1.0
S × S	13.55 ± 0.06	201.1 ± 2.2	100.8 ± 1.0
H × D	13.36 ± 0.19	200.5 ± 7.8	104.7 ± 3.5
D × H	13.33 ± 0.23	203.2 ± 10.1	111.4 ± 4.6
P × S	13.48 ± 0.24	181.8 ± 8.8	101.2 ± 4.0
S × P	13.50 ± 0.23	192.3 ± 8.7	100.3 ± 4.0
S × H	13.37 ± 0.14	193.3 ± 5.4	102.0 ± 2.4
H × S	13.56 ± 0.13	192.4 ± 5.9	109.5 ± 2.7
S × D	13.52 ± 0.20	203.8 ± 8.9	103.9 ± 4.0
D × S	13.41 ± 0.22	206.9 ± 10.4	117.3 ± 4.7
P × D	13.00 ± 0.12	189.2 ± 4.4	96.5 ± 2.0
D × P	12.64 ± 0.14	191.1 ± 5.9	100.4 ± 2.7
P × H	12.45 ± 0.25	198.8 ± 9.8	99.0 ± 4.5
H × P	13.26 ± 0.22	190.9 ± 9.4	104.5 ± 4.3
SH × PD	13.58 ± 0.14	198.4 ± 5.0	102.2 ± 2.3
SH × DP	13.68 ± 0.15	186.6 ± 5.3	99.9 ± 2.4
PD × SH	13.34 ± 0.15	210.8 ± 6.1	105.5 ± 2.8
PD × HS	13.27 ± 0.15	201.4 ± 5.7	105.0 ± 2.6
HP × SD	13.18 ± 0.23	202.8 ± 8.5	108.1 ± 3.9
HP × DS	12.95 ± 0.22	195.5 ± 8.0	104.8 ± 3.6
DS × PH	13.22 ± 0.23	191.7 ± 9.0	102.6 ± 4.1
DS × HP	13.16 ± 0.22	185.6 ± 8.5	102.8 ± 3.9
DH × SP	13.23 ± 0.23	198.0 ± 8.8	106.0 ± 4.0
DH × PS	13.13 ± 0.21	215.4 ± 8.7	112.9 ± 4.0
SP × DH	13.65 ± 0.22	207.1 ± 9.1	105.3 ± 4.1
SP × HD	13.04 ± 0.22	218.4 ± 8.2	108.7 ± 3.7
F_2[b]	13.72 ± 0.18	202.6 ± 6.6	99.5 ± 3.0
F_2[c]	13.40 ± 0.17	198.9 ± 5.4	103.1 ± 2.5
F_3	13.80 ± 0.06	192.6 ± 1.9	98.9 ± 0.9

[a]H = Hampshire, D = Duroc, P = Pietrain, and S = Spot. The first letter indicates breed of sire and the second letter indicates breed of dam. F_3, F_4, F_5, and F_6 were pooled. Progeny of reciprocal two-breed dams were classified separately to account for maternal grandam breed effects, but progeny of reciprocal two-breed cross sires were pooled.
[b]F_2 animals with SH or HS maternal grandams.
[c]F_2 animals with DP or PD maternal grandams.

Appendix Table 3. Least-squares means and standard errors of breed types for gestation length, sow weight at 110 d of gestation, sow weight at weaning, and lactation weight loss in Experiment 1

Breed type[a]	Gestation length, d	d 110 wt, kg	Wt at weaning, kg	Lactation wt loss, kg
Y × Y(pb)	115.11 ± 0.18	147.4 ± 1.8	135.0 ± 1.7	−12.5 ± 1.4
L × L(pb)	114.48 ± 0.17	155.0 ± 1.7	136.8 ± 1.7	−18.2 ± 1.4
W × W(pb)	114.29 ± 0.19	152.3 ± 1.8	141.4 ± 1.8	−11.0 ± 1.5
C × C(pb)	115.16 ± 0.20	152.4 ± 1.9	140.9 ± 1.9	−12.6 ± 1.6
Y × Y(cb)	114.38 ± 0.43	154.7 ± 4.4	135.3 ± 4.4	−19.8 ± 3.6
L × L(cb)	113.85 ± 0.29	155.6 ± 2.8	134.0 ± 2.8	−21.3 ± 2.3
W × W(cb)	114.76 ± 0.27	159.2 ± 2.7	141.5 ± 2.7	−17.0 ± 2.2
C × C(cb)	114.69 ± 0.48	158.4 ± 4.0	136.7 ± 4.2	−21.9 ± 3.4
Y × L	114.41 ± 0.31	153.5 ± 3.1	135.3 ± 3.1	−19.1 ± 2.5
L × Y	114.11 ± 0.65	160.5 ± 6.4	140.5 ± 6.5	−20.1 ± 5.2
Y × W	115.67 ± 0.66	152.2 ± 6.5	139.6 ± 7.1	−17.4 ± 5.8
W × Y	114.58 ± 0.83	150.4 ± 8.1	128.6 ± 8.0	−22.0 ± 6.5
L × W	114.43 ± 0.79	164.6 ± 7.8	157.1 ± 7.8	−7.0 ± 6.3
W × L	114.36 ± 0.64	159.2 ± 6.2	129.1 ± 6.5	−28.0 ± 5.3
W × C	114.28 ± 0.69	163.8 ± 6.7	142.7 ± 6.6	−20.7 ± 5.4
C × L	113.39 ± 0.68	167.2 ± 6.7	141.3 ± 6.6	−26.2 ± 5.4
L × C	113.71 ± 0.65	162.4 ± 6.4	138.0 ± 6.5	−24.4 ± 5.2
C × Y	114.91 ± 0.70	168.5 ± 6.9	138.8 ± 7.0	−29.4 ± 5.6
Y × C	114.19 ± 0.72	151.3 ± 7.1	131.1 ± 7.1	−20.8 ± 5.7
C × W	113.77 ± 0.34	171.5 ± 3.4	150.5 ± 3.6	−23.0 ± 2.9
YL × CW	114.41 ± 0.44	165.8 ± 4.2	143.9 ± 4.3	−19.7 ± 3.5
CW × YL	115.17 ± 0.45	167.5 ± 4.3	149.6 ± 4.3	−16.7 ± 3.5
F_2[b]	114.47 ± 0.40	160.0 ± 3.9	139.3 ± 3.7	−20.7 ± 3.1
F_2[c]	114.36 ± 0.38	153.9 ± 3.7	133.7 ± 3.6	−20.7 ± 3.0
F_3	114.20 ± 0.18	164.4 ± 1.7	141.1 ± 1.7	−23.5 ± 1.4

[a]Y = Yorkshire, L = Landrace, W = Large White, and C = Chester White. The first letter indicates breed of sire and the second letter indicates breed of dam. Purebred females produced either purebred (pb) or crossbred (cb) litters. F_3, F_4, and F_5 were pooled. Progeny of reciprocal two-breed dams were classified separately to account for maternal grandam breed effects, but progeny of reciprocal two-breed cross sires were pooled.

[b]F_2 animals with YL maternal grandams.

[c]F_2 animals with CW maternal grandams.

Appendix Table 4. Least-squares means and standard errors of breed types for gestation length, sow weight at 110 d of gestation, sow weight at weaning, and lactation weight loss in Experiment 2

Breed type[a]	Gestation length, d	110 d wt, kg	Wt at weaning, kg	Lactation wt loss, kg
H × H(pb)	113.39 ± 0.20	149.9 ± 1.8	136.6 ± 2.1	−14.4 ± 1.5
D × D(pb)	113.07 ± 0.20	157.8 ± 1.8	146.2 ± 2.1	−12.0 ± 1.5
P × P(pb)	114.42 ± 0.17	133.8 ± 1.6	122.7 ± 1.8	−11.7 ± 1.3
S × S(pb)	114.28 ± 0.17	153.6 ± 1.6	141.1 ± 1.9	−12.0 ± 1.4
H × H(cb)	113.85 ± 0.30	150.4 ± 2.7	135.2 ± 3.3	−16.1 ± 2.4
D × D(cb)	113.01 ± 0.29	155.6 ± 2.7	138.1 ± 3.1	−17.0 ± 2.2
P × P(cb)	113.94 ± 0.43	142.8 ± 4.0	128.5 ± 4.7	−14.1 ± 3.5
S × S(cb)	113.99 ± 0.41	160.6 ± 3.9	143.9 ± 4.3	−14.4 ± 3.3
H × D	113.43 ± 0.61	163.4 ± 5.8	147.8 ± 6.4	−15.2 ± 5.0
D × H	113.43 ± 0.67	168.6 ± 6.3	145.9 ± 7.0	−22.9 ± 5.2
P × S	113.57 ± 0.64	164.1 ± 6.0	135.7 ± 6.7	−27.7 ± 5.1
S × P	113.84 ± 0.69	161.9 ± 6.5	144.6 ± 7.3	−17.2 ± 5.5
S × H	113.86 ± 0.42	160.6 ± 4.0	137.8 ± 4.8	−21.0 ± 3.8
H × S	114.13 ± 0.45	166.9 ± 4.2	142.0 ± 4.7	−23.9 ± 3.6
S × D	113.06 ± 0.69	170.0 ± 6.4	148.3 ± 7.2	−22.1 ± 5.5

D × S	113.02 ± 0.71	166.6 ± 6.6	148.3 ± 7.4	–18.6 ± 5.4
P × D	113.87 ± 0.38	156.4 ± 3.5	127.1 ± 4.0	–28.3 ± 3.1
D × P	113.43 ± 0.43	153.6 ± 4.0	128.9 ± 4.5	–24.0 ± 3.3
P × H	113.37 ± 0.65	155.8 ± 6.1	137.1 ± 6.8	–18.6 ± 5.1
H × P	112.67 ± 0.63	165.1 ± 5.9	144.0 ± 6.6	–21.4 ± 5.0
SH × PD	113.66 ± 0.57	165.8 ± 5.3	144.4 ± 6.0	–22.6 ± 4.5
SH × DP	113.26 ± 0.49	155.0 ± 4.5	134.8 ± 5.1	–20.1 ± 3.6
PD × SH	113.14 ± 0.63	156.0 ± 5.9	135.1 ± 6.6	–21.5 ± 5.0
PD × HS	113.58 ± 0.67	157.6 ± 6.3	135.1 ± 7.0	–22.9 ± 5.4
F_2[b]	113.60 ± 0.46	157.4 ± 4.2	135.9 ± 4.9	–21.6 ± 3.6
F_2[c]	113.24 ± 0.37	159.2 ± 3.3	137.6 ± 3.8	–21.2 ± 2.7
F_3	113.73 ± 0.17	160.7 ± 1.6	140.2 ± 1.8	–20.4 ± 1.3

[a]H = Hampshire, D = Duroc, P = Pietrain, and S = Spot. The first letter indicates breed of sire and the second letter indicates breed of dam. Purebred females produced either purebred (pb) or crossbred (cb) litters. F_3, F_4, and F_5 were pooled. Progeny of reciprocal two-breed dams were classified separately to account for maternal grandam breed effects, but progeny of reciprocal two-breed cross sires were pooled.
[b]F_2 animals with SH or HS maternal grandams.
[c]F_2 animals with DP or PD maternal grandams.

Appendix Table 5. Least-squares means and standard errors of breed types for litter sizes and weights in Experiment 1

	Number of pigs				Litter wt, kg		
Breed type[a]	Fully formed	Born live	14 d	Weaned	Birth	14 d	28 d
Y × Y(pb)	8.25 ± 0.31	7.50 ± 0.32	6.68 ± 0.33	6.58 ± 0.32	9.02 ± 0.38	21.42 ± 1.08	39.65 ± 1.80
L × L(pb)	9.34 ± 0.30	8.83 ± 0.30	7.68 ± 0.31	7.48 ± 0.31	13.02 ± 0.36	26.76 ± 1.04	45.93 ± 1.74
W × W(pb)	8.13 ± 0.32	7.57 ± 0.32	6.33 ± 0.33	6.19 ± 0.33	9.18 ± 0.39	20.77 ± 1.11	37.81 ± 1.85
C × C(pb)	8.55 ± 0.34	7.79 ± 0.34	5.68 ± 0.35	5.50 ± 0.35	9.88 ± 0.41	17.57 ± 1.17	32.33 ± 1.95
Y × Y(cb)	8.74 ± 0.77	8.41 ± 0.78	7.39 ± 0.81	7.34 ± 0.81	10.17 ± 0.94	25.42 ± 2.70	44.18 ± 4.51
L × L(cb)	9.38 ± 0.49	8.92 ± 0.50	8.11 ± 0.52	8.07 ± 0.52	13.50 ± 0.60	29.32 ± 1.75	50.69 ± 2.91
W × W(cb)	7.83 ± 0.47	7.44 ± 0.47	6.52 ± 0.49	6.53 ± 0.49	9.91 ± 0.57	24.00 ± 1.64	43.00 ± 2.74
C × C(cb)	8.90 ± 0.82	8.68 ± 0.83	7.54 ± 0.86	7.55 ± 0.86	10.95 ± 1.00	26.62 ± 2.87	46.01 ± 4.79
Y × L	8.59 ± 0.52	8.44 ± 0.54	8.25 ± 0.57	8.18 ± 0.56	11.79 ± 0.65	31.42 ± 1.90	56.12 ± 3.16
L × Y	8.90 ± 1.10	8.92 ± 1.12	8.48 ± 1.20	8.48 ± 1.18	12.23 ± 1.35	30.80 ± 3.97	54.33 ± 6.61
Y × W	6.32 ± 1.12	6.34 ± 1.14	6.08 ± 1.21	6.10 ± 1.20	9.10 ± 1.37	24.62 ± 4.03	42.39 ± 6.71
W × Y	7.77 ± 1.41	7.55 ± 1.43	6.75 ± 1.50	6.74 ± 1.49	11.73 ± 1.72	25.01 ± 5.00	45.46 ± 8.34
L × W	4.24 ± 1.33	4.46 ± 1.36	4.48 ± 1.44	4.48 ± 1.43	6.79 ± 1.64	20.47 ± 4.81	38.35 ± 8.01
W × L	8.48 ± 1.09	8.25 ± 1.11	6.86 ± 1.16	6.86 ± 1.15	12.22 ± 1.33	29.15 ± 3.85	52.04 ± 6.42
W × C	9.75 ± 1.17	10.00 ± 1.19	9.37 ± 1.25	9.37 ± 1.24	12.93 ± 1.43	34.38 ± 4.15	60.57 ± 6.91
C × L	9.84 ± 1.16	9.93 ± 1.18	9.50 ± 1.24	9.46 ± 1.23	13.11 ± 1.42	33.51 ± 4.13	59.73 ± 6.88
L × C	8.33 ± 1.10	8.52 ± 1.12	8.12 ± 1.19	8.12 ± 1.18	11.79 ± 1.35	29.76 ± 3.97	53.56 ± 6.61
C × Y	11.10 ± 1.17	10.66 ± 1.20	9.57 ± 1.28	9.17 ± 1.27	13.45 ± 1.45	30.04 ± 4.28	52.09 ± 7.13
Y × C	8.79 ± 1.21	8.96 ± 1.23	8.76 ± 1.31	8.55 ± 1.30	11.74 ± 1.49	30.91 ± 4.37	52.70 ± 7.28
C × W	9.73 ± 0.58	9.11 ± 0.59	7.90 ± 0.63	7.79 ± 0.62	12.14 ± 0.71	27.41 ± 2.10	49.28 ± 3.49
YL × CW	9.31 ± 0.75	9.11 ± 0.76	7.73 ± 0.79	7.70 ± 0.78	11.99 ± 0.91	28.30 ± 2.62	50.19 ± 4.37
CW × YL	10.05 ± 0.76	9.42 ± 0.77	7.61 ± 0.81	7.57 ± 0.80	12.37 ± 0.93	26.06 ± 2.69	48.78 ± 4.48
F_2[b]	9.81 ± 0.69	9.21 ± 0.70	7.90 ± 0.72	7.84 ± 0.71	12.05 ± 0.84	28.54 ± 2.38	52.75 ± 3.98
F_2[c]	8.16 ± 0.67	7.61 ± 0.67	6.95 ± 0.69	6.86 ± 0.68	11.28 ± 0.80	26.92 ± 2.28	48.25 ± 3.81
F_3	9.50 ± 0.32	8.89 ± 0.32	8.05 ± 0.33	8.01 ± 0.32	12.25 ± 0.38	28.81 ± 1.08	51.12 ± 1.81

[a]Y = Yorkshire, L = Swedish Landrace, W = Large White, and C = Chester White. The first letter indicates breed of sire and the second letter indicates breed of dam. Purebred females produced either purebred (pb) or crossbred (cb) litters. F_3, F_4, and F_5 were pooled. Progeny of reciprocal two-breed dams were classified separately to account for maternal grandam breed effects, but progeny of reciprocal two-breed cross sires were pooled.
[b]F_2 animals with YL maternal grandams.
[c]F_2 animals with CW maternal grandams.

Appendix Table 6. Least-squares means and standard errors of breed types for litter sizes and weights in Experiment 2

	Number of pigs				Litter wt, kg		
Breed type[a]	Fully formed	Born live	14 d	Weaned	Birth	14 d	28 d
H × H(pb)	7.74 ± 0.30	7.28 ± 0.31	5.98 ± 0.32	5.82 ± 0.32	9.49 ± 0.37	18.57 ± 1.04	34.08 ± 1.78
D × D(pb)	8.85 ± 0.31	8.04 ± 0.31	6.45 ± 0.33	6.16 ± 0.32	10.85 ± 0.37	19.40 ± 1.06	33.44 ± 1.81
P × P(pb)	6.98 ± 0.26	6.37 ± 0.27	5.39 ± 0.27	5.16 ± 0.27	8.60 ± 0.32	16.77 ± 0.89	29.05 ± 1.53
S × S(pb)	7.73 ± 0.26	7.13 ± 0.27	4.57 ± 0.27	4.52 ± 0.28	10.47 ± 0.32	15.48 ± 0.90	27.74 ± 1.54
H × H(cb)	7.45 ± 0.45	7.11 ± 0.46	5.47 ± 0.47	5.39 ± 0.47	8.89 ± 0.55	18.08 ± 1.53	33.46 ± 2.63
D × D(cb)	8.37 ± 0.44	7.89 ± 0.45	7.27 ± 0.45	7.16 ± 0.45	11.09 ± 0.54	23.37 ± 1.48	40.73 ± 2.53
P × P(cb)	6.70 ± 0.67	5.87 ± 0.68	4.92 ± 0.71	4.91 ± 0.71	8.88 ± 0.81	18.94 ± 2.31	34.48 ± 3.95
S × S(cb)	6.83 ± 0.62	6.28 ± 0.64	4.30 ± 0.66	4.22 ± 0.66	10.11 ± 0.76	17.32 ± 2.14	32.30 ± 3.67
H × D	8.85 ± 1.00	8.23 ± 1.02	7.24 ± 1.10	7.25 ± 1.09	11.18 ± 1.21	24.63 ± 3.58	43.74 ± 6.09
D × H	9.84 ± 1.05	9.32 ± 1.08	8.11 ± 1.13	8.14 ± 1.12	12.50 ± 1.28	27.12 ± 3.67	48.64 ± 6.27
P × S	9.71 ± 1.02	9.23 ± 1.05	8.42 ± 1.11	8.43 ± 1.11	15.22 ± 1.24	34.10 ± 3.62	57.45 ± 6.17
S × P	8.30 ± 1.11	7.97 ± 1.13	7.11 ± 1.21	6.90 ± 1.20	12.84 ± 1.34	30.26 ± 3.92	52.12 ± 6.68
S × H	8.70 ± 0.70	8.19 ± 0.71	6.20 ± 0.77	6.20 ± 0.76	11.76 ± 0.84	21.45 ± 2.50	38.08 ± 4.25
H × S	10.14 ± 0.73	9.62 ± 0.75	8.42 ± 0.80	8.33 ± 0.80	13.13 ± 0.89	26.82 ± 2.62	47.98 ± 4.45
S × D	9.54 ± 1.10	9.27 ± 1.13	8.06 ± 1.20	7.64 ± 1.20	14.59 ± 1.34	27.86 ± 3.92	46.60 ± 6.68
D × S	9.29 ± 1.09	8.92 ± 1.12	7.98 ± 1.14	8.01 ± 1.15	13.03 ± 1.34	27.61 ± 3.73	51.80 ± 6.40
P × D	9.63 ± 0.61	9.19 ± 0.63	7.60 ± 0.68	7.51 ± 0.67	13.24 ± 0.74	27.13 ± 2.20	45.38 ± 3.74
D × P	10.75 ± 0.66	9.94 ± 0.68	9.08 ± 0.71	9.00 ± 0.70	15.05 ± 0.81	30.53 ± 2.30	52.02 ± 3.93
P × H	7.78 ± 1.03	6.80 ± 1.06	6.40 ± 1.12	6.41 ± 1.11	10.66 ± 1.26	24.04 ± 3.63	43.71 ± 6.20
H × P	9.50 ± 1.01	9.33 ± 1.04	8.08 ± 1.11	8.09 ± 1.10	12.40 ± 1.23	27.57 ± 3.60	49.33 ± 6.13
SH × PD	10.86 ± 0.89	10.51 ± 0.91	8.45 ± 0.97	8.00 ± 0.96	13.79 ± 1.09	28.54 ± 3.14	47.40 ± 5.36
SH × DP	10.06 ± 0.71	9.48 ± 0.73	7.70 ± 0.72	7.32 ± 0.73	13.55 ± 0.88	26.07 ± 2.36	45.76 ± 4.07
PD × SH	10.17 ± 1.01	10.15 ± 1.03	8.99 ± 1.10	8.75 ± 1.09	13.86 ± 1.22	28.62 ± 3.57	48.72 ± 6.08
PD × HS	11.26 ± 1.08	10.47 ± 1.11	9.59 ± 1.19	9.31 ± 1.18	13.85 ± 1.31	29.92 ± 3.87	52.86 ± 6.58
F_2[b]	7.61 ± 0.70	6.70 ± 0.71	5.49 ± 0.74	5.59 ± 0.74	11.32 ± 0.86	22.61 ± 2.40	40.30 ± 4.11
F_2[c]	8.80 ± 0.53	8.39 ± 0.54	6.81 ± 0.54	6.92 ± 0.54	12.78 ± 0.65	25.15 ± 1.76	45.04 ± 3.03
F_3	8.98 ± 0.25	8.35 ± 0.26	7.18 ± 0.26	7.02 ± 0.27	12.17 ± 0.31	24.59 ± 0.86	44.22 ± 1.48

[a]H = Hampshire, D = Duroc, P = Pietrain, and S = Spot. The first letter indicates breed of sire and the second letter indicates breed of dam. Purebred females produced either purebred (pb) or crossbred (cb) litters. F_3, F_4, and F_5 were pooled. Progeny of reciprocal two-breed dams were classified separately to account for maternal grandam breed effects, but progeny of reciprocal two-breed cross sires were pooled.

[b]F_2 animals with SH or HS maternal grandams.

[c]F_2 animals with DP or PD maternal grandams.